AN EXAMPLE OF REVERSAL OF POLARITY DURING ASEXUAL REPRODUCTION OF A HYDROID

CADET HAND AND MEREDITH L. JONES

Department of Zoology, University of California, Berkeley, California

A number of small and curious hydroids have been described over the years. These hydroids, in general, occur on soft bottoms as members of the fauna of the upper few millimeters and are of rather diverse asexual reproductive habits. This group, most of which are unrelated systematically, includes *Boreohydra, Psammohydra, Corymorpha, Heteractis, Euphysa* (the last three closely related), *Halermita* and *Microhydra*. In view of the apparently wide distribution of this type of hydroid in soft bottom communities it is probably not surprising that still another form has been discovered in San Francisco Bay, California.

On November 28, 1954, we recovered two live specimens of such a hydroid from a core sample 18 mm. in diameter taken at a depth of 30 feet off Pt. Richmond. The bottom at that location consists of grey mud overlain by about 5 mm. of loose debris, from which the hydroid to be described was taken. According to Sumner *et al.* (1914) the annual salinity in this area ranges from 18.0‰ to 32.3‰ with a mean of 27.0‰.

MORPHOLOGY AND REPRODUCTIVE BEHAVIOR

The two specimens were a single polyp and a pair of polyps united at their base. Each had a small patch of debris adherent to its base. Figure 1 illustrates the pair. The polyps were quite extensible and were about 1–1.5 mm. long when maximally extended. The hydrocaulus was narrowest at the base and gradually enlarged toward the area of tentacular insertion, where the diameter was approximately twice that of the more proximal region. The tentacles were filiform and were capable of extending to about 1 mm. They were inserted in a single cycle at the base of the proboscis. The number of tentacles varied from as few as 4 to as many as 12, although, of the original specimens, the solitary individual had 6 and the pair had 9 and 10 at the time they were first observed. Due to the extreme contractility and extensibility of the hydroid, the relative length of the proboscis and the hydrocaulus was quite variable. In general, however, this relationship varied from 1 : 1 to 1 : 3 (*i.e.*, with the hydrocaulus about three times the length of the proboscis, at times). The color of the hydroids was a light, flesh-pink, and the whole animal was translucent.

The two original specimens were set aside in a stender dish to which was added a small amount of debris from the core sample. The specimens were observed at least once a week following this and were fed the nauplii of brine shrimp (*Artemia*) at each observation. Early in January it was noted that there were two pairs of polyps plus the single one in the culture dish. At the time it was assumed that the extra pair had been overlooked at the time of isolation. However, on January 24,
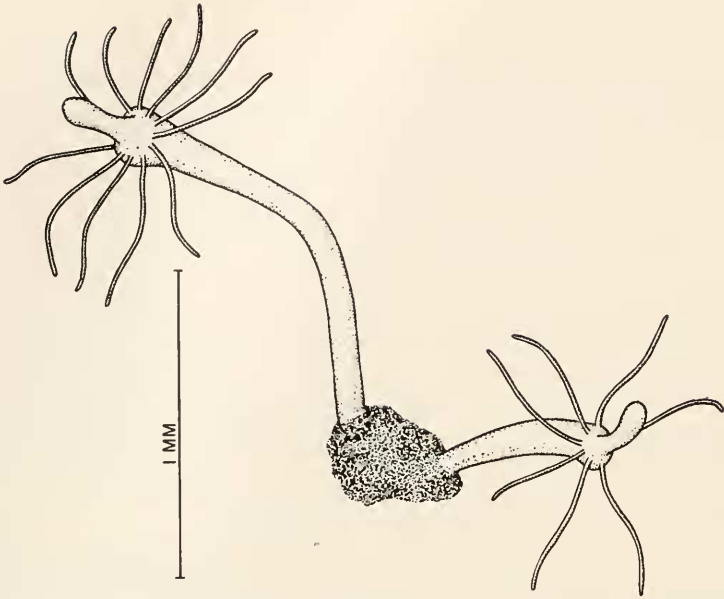
FIGURE 1. The original paired hydranths. The individual on the left has elongated preparatory to undergoing asexual division.
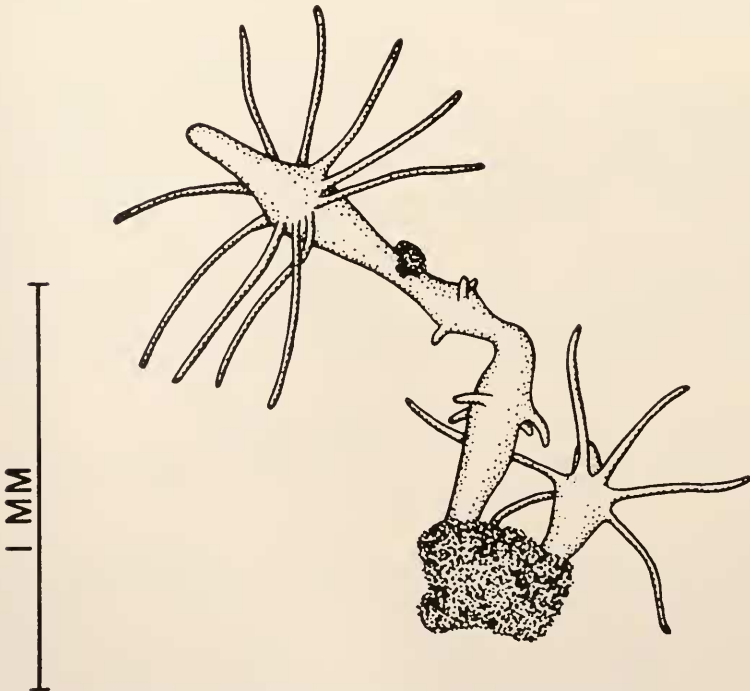

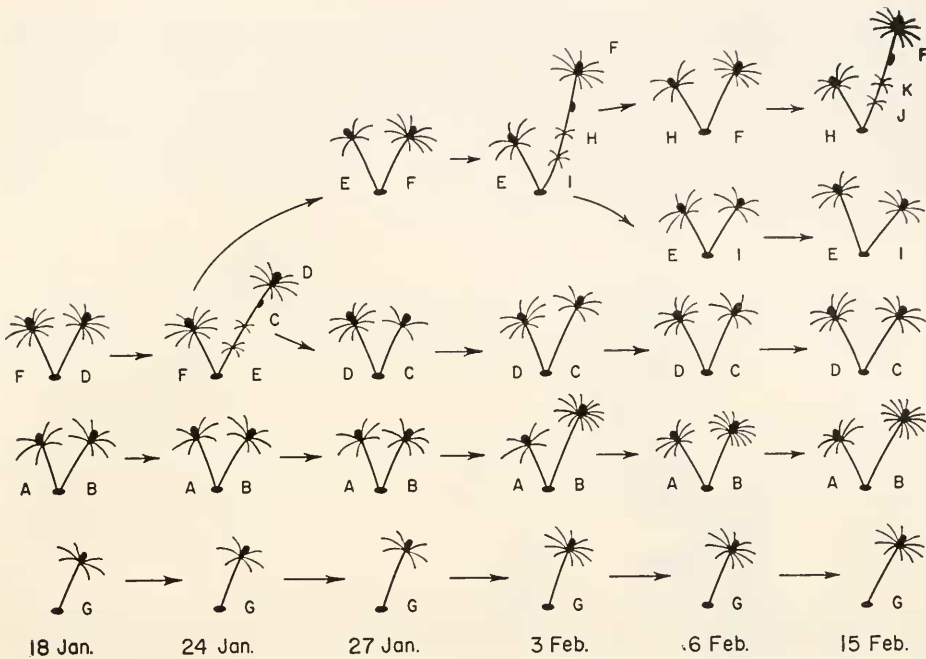FIGURE 2. A polyp pair in process of asexual division.

FIGURE 3.   A schematic diagram showing results of observations on critical dates from January 18 to February 15, 1955.

1955, it was observed that a polyp of one of the pairs had become about twice the length of its partner and possessed two additional sets of tentacles, intercalated between the base and the original whorl of tentacles, and further, at a point between the new tentacles and old hydranth, debris had collected and was adherent to the hydrocaulus (Fig. 2).   Daily observations following this made it clear that we were witnessing an unusual mode of asexual reproduction which resulted in the production of pairs of polyps.   By January 27, fission had occurred between the two new sets of tentacles, and the area of adherent debris had become the base of the new polyp pair.   Pursuant to this discovery we began a series of daily observations extending from January 24 to February 15.

For convenience in record-keeping, letters were assigned to the polyps (these letters will be referred to in the text, where necessary), and the accompanying figure (Fig. 3) illustrates, in a diagrammatic fashion, the results of our observations from January 18 to February 15.   At this time there were four pairs and a single polyp. The polyps "F" and "D" were the only polyps to divide during this period, and one of these probably gave rise to polyp pair "A-B."   In each instance the elapsed time between the first appearance of new tentacles and actual divisions was three days.

Following February 15 our observations became somewhat irregular, and a single observation on March 4 revealed that we now had seven pairs of polyps and that two of the pairs were preparing to divide once more (the single specimen had been sacrificed previously for nematocyst data).   Immediately following this observation, the dish containing the hydroids became badly fouled (presumably as a re-

sult of over-feeding with *Artemia* larvae, and our subsequent failure to change the water), and on March 8, when this was discovered, the remaining hydroids were in what appeared to be very poor condition. Each polyp was tightly contracted to about one-third its normal height and was about 0.5 mm. in diameter. The tentacles were mere knobs and the animals had assumed a nearly hemispherical form. The water was changed, but this failed to save most of the specimens and by March 15 we were left with but a single pair of polyps.
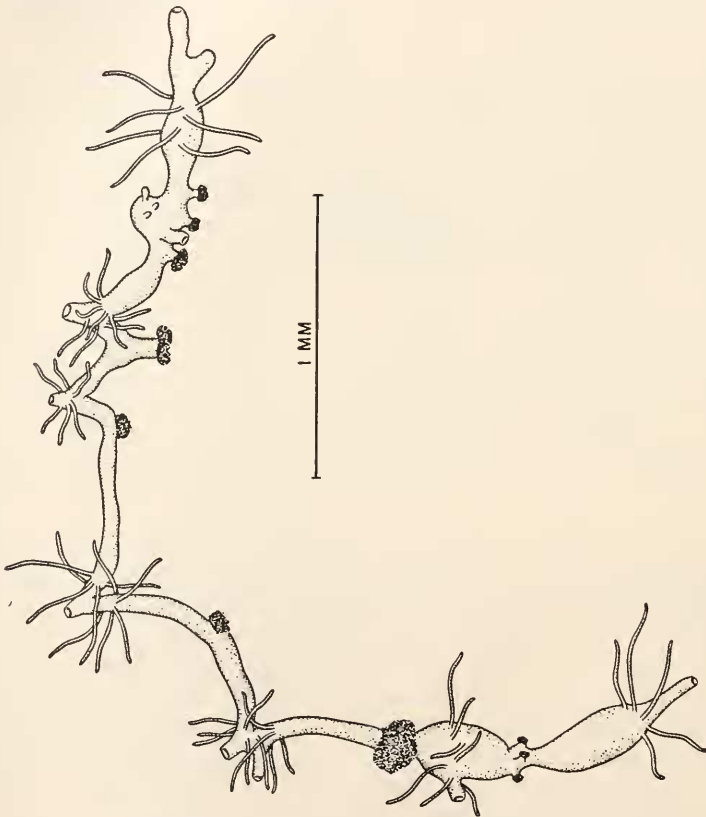

FIGURE 4.   The monstrosity on March 25.

On March 21 we observed that our remaining pair had once more produced two new polyps, but although these were well-formed, they still had not separated. On the next day (March 22), although the two new polyps had not yet parted, there were signs that still another pair of polyps was being formed, giving us six polyps in series, and this specimen was apparently becoming a monstrosity. We also noted that near the middle of the central hydrocaulus there was a single protuberance and a group of four structures which looked like still another pair of incipient polyps with irregularly placed tentacles. By the next day (March 23) our specimen had opened another mouth between a pair of orally-directed polyps and we could now count 12 sets of tentacles and 4 open mouths. By March 25 the animal had grown

to about 4.5 mm. long (Fig. 4), was composed of 14 recognizable individuals and had 8 mouths which seemed to be functional (in that they were seen to open and close and brine shrimp larvae were ingested by several).

On March 28 the specimen had finally succeeded in dividing into pieces, and we were able to count two single polyps, two separate double polyps, one triple polyp (three mouths and sets of tentacles with a single base), one quadruple (four mouths, three sets of tentacles and a base), and two groups of polyps which had three and four mouths each. These last two groups consisted of rather curious assemblages of mouths, misplaced tentacles, and bits of adherent debris (suggesting bases) at irregular points over the masses.

This situation, that is, with eight variously assorted hydroids ranging from single individuals to groups of four, was maintained without further change until April 4. Following this date, the numbers were reduced by death, and by June 1, all the individuals had died.

As stated above, during the earlier part of our study, the original single polyp (polyp "G," Fig. 3) was sacrificed to study its nematocysts, and, unfortunately, none of the polyps or polyp pairs was preserved. Although we have taken more than 1200 core samples from the general area of the original collection, none have been found since.

Description of Asexual Reproduction

The sequence of events leading to the production of new pairs of polyps in this hydroid has been closely observed. The earliest sign that the process was underway
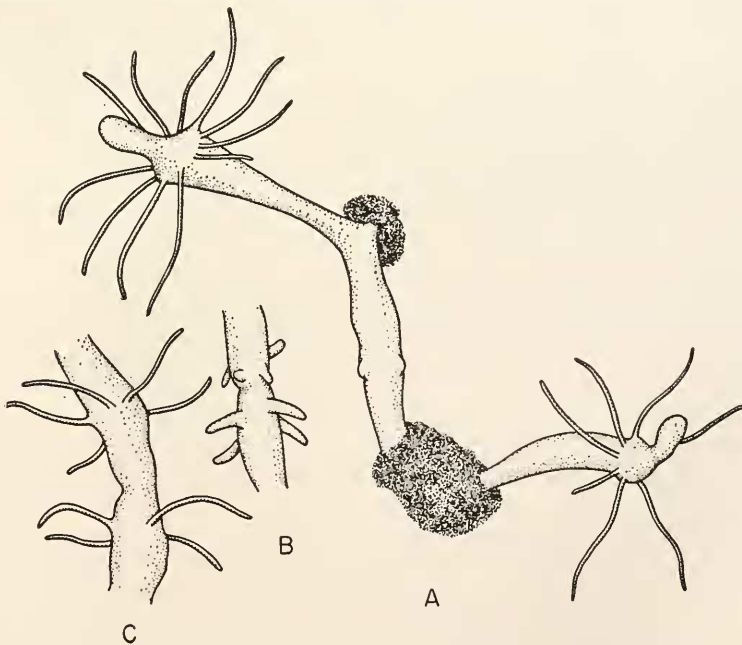

Figure 5. Development of tentacles prior to asexual division. A, the polyp pair with new tentacles barely recognizable (February 14); B, tentacle growth in 23 hours (February 15); C, tentacle growth in 40 hours (February 16).

was the adherence of a small bit of debris to the hydrocaulus at about its mid-point, although this was commonly nearer the tentacles than the base (Fig. 5, A). This phenomenon was associated with a slight increase in the opacity of the tissues at this point, and the protrusion of a small knob of tissue. This knob within 24 hours of its appearance became completely obscured by adherent debris. In addition, during this first phase of development, two sets of minute protuberances were seen in the mid-region of the hydrocaulus, between the adherent debris and the original base (Fig. 5, A). Within 24 hours, the protuberances grew into recognizable tentacles, usually three or four per whorl (Fig. 5, B). With the appearance of the tentacles, there is a marked increase in the opacity of the tissue in this area.

During the second 24-hour period, a translucent region developed in the area between the two new sets of tentacles, and subsequently, there was an indenting of the surface tissue of the hydrocaulus at this point. On the third day, there was a further continuation of the constriction of this area, leading to the actual separation of the two new polyps. This point of fission marked the distal end of the proboscis of each of the two new polyps, and each polyp possessed a functional mouth as soon as fission was completed; in addition, the point of adherent debris had now become the base of the newly released pair. The result of this process of fission was two pairs of polyps, each with one member (the older) about one-third larger than the new polyp.

Discussion

Many well-known studies have established the fact that hydroids possess gradients, particularly those of regenerative ability, which are more marked or rapid in more distal pieces of stems. Steinberg (1954), in studies on *Tubularia,* found that short pieces of stem (1–2 mm. long) regenerate bipolar or partial bipolar hydranths, while in longer pieces (2–12 mm.) a new hydranth is usually formed only at the original distal end of the stem, and, in still longer pieces (12–30 mm.), each end regenerates a hydranth. Steinberg also describes movements of cells toward the distal ends of cut stems and states that these cell movements precede the process of regeneration. In the hydroid described above, since the whole animal is less than 2 mm. long, one wonders if there can be effective or actual gradients such as those obviously present in larger hydroids. However, numerous studies on *Hydra,* an equally small organism, have shown that well-developed gradients also exist in small hydroids. In the animal described here, the appearance of two new orally-directed hydroids interposed in series between an extant base and hydranth must mean that a re-organization, involving a reversal of the original polarity of the hydrocaulus, has occurred, and it would seem that information obtained from experimental studies already completed on other hydroids should help to explain this observed event.

It should be pointed out that the reversal of polarity, which we assume to be present during the course of asexual reproduction, is a unique event. Hyman (1940, pp. 487–492) has reviewed much of the literature to that date relative to asexual reproduction and regulative processes in hydroids. She points out that in animals as small as hydras the polarity is well-developed and can only be altered by rather drastic treatments, *i.e.,* electrical currents, burial of the apical end of a cut stem, or by treatment with cyanides, anesthetics, and other depressing chemicals. Further, it is well known that pieces of hydroid stems and hydras retain their original polarity whether free or grafted to other pieces. We assume, therefore, that our

animal must also have a definite basal-oral polarity; that in the course of asexual reproduction by this animal, the polarity is reversed, at least for a short part of the hydrocaulus; and that this is a naturally-occurring and unusual event.

After considering all the evidence available to us, we have come to the conclusion that we can explain our observations on this hydroid if we are allowed to make one hypothesis. This hypothesis is concerned with the first event we observed during the course of asexual reproduction (*i.e.*, adherence of debris to the hydrocaulus) and is unique to the extent that it gives certain unusual features to the presumptive base of the new polyp pair. We suggest that the appearance or formation of the new base, as the first step in asexual reproduction here, must represent an effective block in the existing gradient, and that this new base must compete (in a certain sense) with the old base for the hydrocaulus between them. Since it is well-established that distal portions of hydroid stems form new hydranths, we can now consider that the portion of the stem between the bases is distal to each base and that it proceeds to develop two new orally-directed polyps simultaneously. In other words, we believe that the two bases with the common piece of hydrocaulus between them, are, individually, behaving in the same fashion as would pieces of decapitate stem, *i.e.*, that there will be regeneration of a new hydranth at the distal extremity. This, of course, must involve a reversal of the preëxisting gradient in the piece of hydrocaulus closest to the newly formed base, and we might postulate that this is the result of some disorganizational or re-organizational power of the base. To the extent that we observed a condensation or increasing opacity in the tissues at the points of formation of the two new polyps, our observations seem to fit the known facts, such as those presented by Steinberg (1954). If, therefore, our hypothesis is acceptable, we can interpret asexual reproduction in this hydroid as a phenomenon involving regeneration at distal extremities.

Cases of reversal of polarity do not seem to have been reported in nature for any other hydroids, unless we can interpret the study of Rees (1937) on *Heterostephanus* (now *Heteractis aurata* according to Kramp, 1949) as such. In *H. aurata* the polyp bud develops from the side of a hydranth, usually a tentacle base, in such a fashion that the free end of the bud is the future hydrocaulus. This same phenomenon has been observed by us in a similar hydroid (*Euphysa* sp.) from San Francisco Bay. In all other cases where transverse fission occurs, a new polyp develops at the distal end of the remaining hydrocaulus, and the new free individual develops a base at the proximal end of its own hydrocaulus. In one genus, *Psammohydra*, Schulz (1950) has found that the new hydranth develops tentacles before fission actually takes place.

Recently Kinne (1956) has made observations on *Cordylophora caspia,* an athecate hydroid from fresh and brackish water. He noted that in approximately 20% of polyps adapted to a salinity of 24‰ , there were various abnormalities developed. These consisted of : the formation of intercalary hydranths on a hydrocaulus ("uniaxial hydranth aggregates"); fusion of polyps ("multiaxial hydranth aggregates"); the formation of large coenenchymal bodies, which became detached from the colony and formed new hydranths; and "globular hydranth complexes," with no stolons and no stalks.

The formation of the intercalary polyps is remarkably similar to the phenomenon observed in the hydroids from San Francisco Bay. However, there are points of difference, for in *Cordylophora*, the two new polyps are joined by the sides of the

hypostome and the mouths are directed laterally, the original polyp is a member of a colony, and there is no interruption of the hydrocaulus between the old and new polyp head which might correspond to the new base of our local forms. Kinne mentions that when the hydranth groups are detached they frequently become established on the substrate and sprout new stalks, but no intimation is made that these persist as pairs, nor that further intercalary hydranths are formed.

In an early section of this report we described a monstrosity which developed from a pair of polyps following their recovery from a period of depression. Hyman (1940) has reviewed the general effects of depression on hydroids, and notes that after recovery from depression, hydras often regenerate doubled parts or other anomalies, and that this is followed by fission processes. Kinne explains his various anomalous forms as the results of disturbances of growth and differentiation processes and a consideration of our observations leads us to evaluate our monstrosities in the same light.

However, since we noted some six apparently normal divisions, culminating in seven polyp pairs, and since the original pair was taken in the field and had not, so far as we know, been exposed to abnormal environmental conditions, we reserve judgment as to whether or not this process is abnormal, for this organism. The possibility does exist that the unknown hydroid, upon which we based our observations, is actually a *Cordylophora,* for this genus has been collected at the Carquinez Straits, approximately 15 miles up the San Francisco Bay Estuary from Point Richmond.

<center>SYSTEMATICS</center>

We have little concrete information to guide us in the identification of the hydroid we have described. Our study of the nematocysts revealed that it possesses a simple cnidom of desmonemes and euryteles, as follows:

Small desmonemes (common)............................4–5 $\times$ 3–4 μ
Large desmonemes (rare).................................9–10 $\times$ 5–4 μ
Microbasic euryteles (common)...........................9–11 $\times$ 3–4 μ

This cnidom suggests that the hydroid is a member of the gymnoblasts (anthomedusae) or limnomedusae (see Weill, 1934; Russell, 1938; Hand, 1954). The complete absence of perisarc also suggests that the hydroid may be a limnomedusan form. However, the perisarc apparently may be completely absent in some gymnoblasts and calyptoblasts. We also know that differences may occur between the cnidom of a hydroid and that of its medusa (Hand, 1954), but in this hydroid, we do not know what medusa, if any, is involved in the life history. Therefore, we can not place this hydroid in any order with certainty, although it seems clear that it can not be a calyptoblast.

Because of the proximity of a source of *Cordylophora,* the possibility of the unknown form's being an abberant type of *Cordylophora* was explored. The main points of difference are that *Cordylophora* grows in extensive colonies, its tentacles are scattered, and it possesses a well-developed perisarc. None of these characters applies to the form described here. In addition, Hand and Gwilliam (1951) reported only a single size-class of desmonemes for *Cordylophora,* while we have found two size-groups. Thus, it seems doubtful that this is actually a growth variant of *Cordylophora.*

Since so little can be done with the hydroid from the standpoint of systematics, we will refrain from assigning it the status of a new species, pending its further collection and a more exact taxonomic determination.

The authors wish to acknowledge the assistance of Mrs. Emily Reid, to whom we are indebted for the illustrations accompanying this report.

SUMMARY

1. Asexual reproduction, involving reversal of the original oral-basal polarity, is described.

2. Asexual reproduction in this hydroid leads to the production of pairs of polyps sharing a common base.

3. The systematic position of the hydroid is not established, although the cnidom suggests possible affinities among the gymnoblasts.

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